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Natural mortality and projected biomass of southern Gulf of St. Lawrence cod (*Gadus morhua*)

Mortalité naturelle de la morue du sud du golfe du Saint-Laurent (*Gadus morhua*) et biomasse projetée

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ABSTRACT

The population of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence collapsed in the early 1990s and has shown no sign of recovery since then despite severely limited fishing mortality. One of the main reasons for this lack of recovery is elevated *M*, the instantaneous rate of natural mortality. Survey-based estimates of total mortality and relative fishing mortality indicate that *M* was very low in the 1970s and had increased to a higher level (0.4 or higher) by the 1990s, possibly increasing to even higher levels since then. Population models which estimate age-aggregated (2+ years) or age-disaggregated (2-4 and 5+) trends in *M* were compared. Models which estimate a single age-aggregated time trend in *M* are not consistent with the data for this stock. Models which estimate separate time trends in *M* for young (age 2-4 yr) and older (5+) cod provide a better fit to the data. Estimated trends in M differ between the two age groups. Estimated *M* declined in the early 1990s for cod aged 2-4 years. For cod aged 5+ yr, *M* was low (near 0.1) in the early 1970s, increased slightly in the late 1970s and early 1980s, then increased sharply in the late 1980s and early 1990s, and has remained at a high level since then. The rapid increase in *M* of 5+ cod as their abundance declined is consistent with the hypothesis that their current high *M* is at least partly a predation-driven Allee effect. At the current levels of *M* and other components of productivity, spawning stock biomass (SSB) is projected to decline steadily even with no fishing, reaching levels near extirpation (SSB<1000 t) in about 40-50 years. Based on the preferred model, in order to have a high probability (*P*) of reaching the limit reference point (SSB=80,000 t) in 20 years, 5+ *M* would have to decrease from the estimated current level of 0.63 to 0.4 or lower if other components of productivity remain unchanged (*P* = 70% for *M* = 0.4, 100% for *M* = 0.35).

RÉSUMÉ

La population de morue (*Gadus morhua*) dans le sud du golfe du Saint-Laurent s'est effondrée au début des années 1990 et ne montre aucun signe de rétablissement depuis cette époque malgré une mortalité par pêche grandement limitée. L'une des principales raisons expliquant cette absence de rétablissement est un coefficient instantané de mortalité naturelle (*M*) élevé. Les estimations de la mortalité totale et de la mortalité relative par pêche fondées sur les relevés indiquent que le coefficient *M* était très faible dans les années 1970 et qu'il a augmenté à un niveau plus élevé (0,4 ou plus) dans les années 1990. Cette augmentation est peut-être encore plus importante depuis. Les modèles de population qui estiment les tendances avec regroupement par âges (2 ans ou plus) et sans regroupement par âges (2 à 4 ans et 5 ans ou plus) du coefficient *M* ont été comparés. Les modèles de population qui estiment une seule tendance temporelle avec regroupement par âges du coefficient *M* ne sont pas compatibles avec ce stock de poissons. En revanche, les modèles qui estiment des tendances temporelles séparées du coefficient *M* pour les morues jeunes (2 à 4 ans) et âgées (5 ans ou plus) correspondent davantage aux données. Les tendances estimées pour le coefficient *M* diffèrent pour les deux groupes d'âge. Le coefficient *M* estimé a diminué au début des années 1990 pour les morues âgées de 2 à 4 ans. Dans le cas de celles âgées de 5 ans ou plus, il était faible (environ 0,1) au début des années 1970, puis a légèrement augmenté à la fin des années 1970 et au début des années 1980. Le coefficient a ensuite connu une augmentation marquée à la fin des années 1980 ainsi qu'au début des années 1990 et est demeuré élevé depuis. L'augmentation rapide du coefficient *M* pour les morues âgées de 5 ans ou plus parallèlement à la diminution de leur abondance est compatible avec l'hypothèse selon laquelle la valeur actuelle élevée du coefficient *M* est au moins en partie due à un effet d'Allee liée à la prédation. En tenant compte du coefficient *M* et des autres aspects de la productivité actuels, la biomasse du stock reproducteur (BSR) devrait diminuer de façon régulière, même sans pêche, au point d'être menacée de disparition (BSR < 1000 t) d'ici 40 à 50 ans. Selon le modèle privilégié, pour que la probabilité (*P*) d'atteindre le point de référence limite (BSR = 80 000 t) dans 20 ans, le coefficient *M* pour les morues de 5 ans ou plus devrait diminuer de la valeur actuelle estimée, soit 0,63, à 0,4 ou moins en supposant que les autres aspects de la productivité demeurent inchangés (*P* = 70 % pour un coefficient *M* = 0,4; 100 % pour un coefficient *M* = 0,35).

1. INTRODUCTION

Many populations of large demersal fishes in the Northwest Atlantic, in particular Atlantic cod (*Gadus morhua*), declined to low levels of abundance in the early 1990s. Some of these populations have failed to recover despite very low fishing mortality. One of these populations is the cod population in the southern Gulf of St. Lawrence. A principle reason for the lack of recovery of this population is high *M*, the instantaneous rate of natural mortality (Swain et al. 2009b).

Coincident with the decline in demersal fish biomass, the abundance of grey seals (*Halichoerus grypus*) in Atlantic Canada has increased dramatically. In October 2010, the Department of Fisheries and Oceans held a workshop to examine possible interactions between grey seals and cod and other large demersal fishes. Among the products required for this workshop were estimates of the trend in natural mortality of cod and of the minimum decrease in natural mortality required to restore cod populations to their limit reference points (LRP). The LRP is the biomass level below which a population is considered to have suffered serious harm to its productivity.

The objectives of this document are to describe the estimated trend in *M* of southern Gulf cod and to estimate the decline in *M* that would be required to allow cod biomass to increase to the LRP with a high probability. Changes in natural mortality are examined both by direct analyses of survey catch rates at age and using population models. The population model used to provide advice in the last assessment of this stock estimated changes in age-aggregated (2+) *M* (Swain et al. 2009b). This document describes population models which estimate separate trends in *M* for ages 2-4 and 5+ years. Based on various diagnostics, these models are preferred over models with age-aggregated *M*. Stochastic projections based on the results of one of these models are used to determine the reduction in 5+ *M* that would be needed to allow recovery to the LRP, assuming that other components of productivity remained at recent levels.

2. MORTALITY ESTIMATES FROM SURVEY CATCH RATES

2.1 INTRODUCTION

A value near 0.2 is generally considered to be the normal level of *M* for Atlantic cod. Estimates for southern Gulf cod based on data collected in the 1970s and earlier tended to be below this value. Using tagging results and commercial catch rates at age, Dickie (1963) concluded that *M* was approximately 0.1 for this stock. Based on growth parameters, Beverton (1965) concluded that *M* was 0.1-0.2 for southern Gulf cod. Using life history data from southern Gulf cod during the 1970s, Myers and Doyle (1983) estimated *M* to be 0.07.

Using a modified catch curve analysis of research vessel (RV) survey data, Sinclair (2001) estimated the instantaneous rate of total mortality (*Z*) in moving blocks of years. Although estimated *Z* dropped sharply with the closure of the fishery in 1993, the estimate for the 1993-1996 period (when there was very little fishing) remained unexpectedly high, suggesting that *M* had increased to a level near 0.4. In this section, I extend this analysis to the present, including catch rates in the sentinel trawl survey conducted since 2003 as well as RV catch rates.

2.2 METHODS

Data are the stratified mean catch rates at age from two stratified-random bottom-trawl surveys, an RV survey conducted each September since 1971 and a sentinel survey conducted each August since 2003. Details on these surveys can be found in Swain et al. (2009b) and references therein.

Following Sinclair (2001), the survey catch rates were analyzed using analysis of covariance. Analyses were conducted in moving 5-yr blocks, with $\log_e$ catch rate as the dependent variable, age as the covariate and year-class included as a factor (to control for variation in year-class strength). The covariate slope in this model provides an estimate of *Z*. Only year-classes with two or more observations in the 5-yr block were retained for analysis. Ages 7-11 were used for these analyses. These ages appear to be approximately fully recruited to these surveys, and residuals showed no pattern with age using this range of ages (e.g., Sinclair 2001). An example of the fit of the statistical model to the data is given in Figure 1. A time series of relative fishing mortality (Sinclair 1998), averaged over the same ages and 5-yr blocks is compared to the time series of *Z* estimates. Relative fishing mortality is catch in numbers divided by survey "trawlable" abundance. Trawlable abundance *N* is defined as:

$$N = n\frac{A}{a}$$

where n is the stratifed mean number of cod (aged 7-11 years, in this case) caught in a standard tow, *a* is the area swept by a standard tow, and *A* is the survey area.

2.3 RESULTS AND DISCUSSION

Based on the RV survey catch rates at age, Z increased sharply in the late 1980s, peaking at values greater than 1 and then dropped sharply with the closure of the fishery in 1993 (Fig. 2). These changes in Z reflected changes in fishing mortality. However, Z remained relatively high following the closure of the fishery in 1993. Based on the RV data, estimated Z was about 0.45-0.55 during the mid to late 1990s, increasing sharply in the 2000s to values between 0.75 and 0.95. The August sentinel trawl data also indicated high Z in the 2000s. The most recent estimates of *Z* from survey catch rates are about 0.6-0.7.

The estimates of *Z* during the fishing moratorium in 1994-1997 indicate that *M* was 0.4 or higher during this period. Estimated *Z* in 1994-1997 was 0.57 (95% CI: 0.47-0.66). Relative fishing mortality (ages 7-11 yr) during this period averaged 0.025. Thus, even assuming that catchability to the survey is 100%, the contribution of estimated fishing mortality to Z during this period is negligible. It might be hypothesized that high Z during this period reflects high levels of unreported catch rather than high M. However, even if fishery removals were three to four times the reported landings during the moratorium (which is unlikely), *M* would need to be 0.4 or higher to account for the estimated Z.

There is no indication that *M* has since decreased below 0.4. The very high *Z* estimates for recent years suggest that natural mortality may have increased to even higher levels, though the uncertainty in the recent estimates is high due to possible year effects in the survey data (Swain et al. 2009b).

Earlier studies obtained estimates for *M* of southern Gulf cod near 0.1 in the 1970s and earlier (Dickie 1963, Beverton 1965, Myers and Doyle 1983). The low estimates of Z in the 1970s

relative to the high estimates of relative fishing mortality (Figure 2) also suggest that *M* was very low in this earlier period.

In summary, survey-based estimates of *Z* and relative *F* indicate 1) that *M* was very low in the 1970s, consistent with the results of other studies from this period, and 2) that *M* had increased to a higher level (0.4 or higher) by the 1990s, possibly increasing to even higher levels since then.

3. ESTIMATES OF NATURAL MORTALITY FROM POPULATION MODELS

3.1 INTRODUCTION

The status of the southern Gulf cod stock is assessed using sequential population analysis (SPA) calibrated using abundance indices from the annual research vessel survey and a number of fishing-industry surveys (e.g., Swain et al. 2009b). Calibration involves finding the parameter estimates that produce the best match between the abundance indices and the SPA estimates of population size. Parameters typically include terminal abundance (i.e., abundance at age in the most recent year) and catchability coefficients for the surveys. Using a simulation study, Chouinard et al. (2005) demonstrated that SPA can also be used to estimate trends in the instantaneous rate of natural mortality (*M*). Following this work, and the demonstration by Sinclair (2001) that *M* was at a high level in this stock during the fishing moratorium in the mid 1990s, recent assessments of this stock have estimated *M* for various blocks of years. These estimates are for all ages (2 years and older) aggregated together.

While SPA can correctly identify the trends in *M* in simulated populations, it sometimes has difficulty identifying the correct level for these trends (Chouinard et al. 2005). Thus the level of *M* should be fixed or "anchored" in some period using ancillary information. In recent assessments of this stock, *M* has been fixed at 0.2 in 1971-1979 based on the independent estimates that *M* was in the range 0.07 to 0.1-0.2 during this period (see references above).

The most recent assessment of this stock compared a number of population models (Swain et al. 2009b):

i. The "standard" model, which estimated age-aggregated *M* in blocks of years and was calibrated using a commercial catch rate index (1982-1993) and a number of relatively short-term fishing-industry (sentinel) surveys (1995-2002, 2003-present, or 1995-present) in addition to indices based on the longer term research vessel (RV) survey (1971-present),
ii. A revised model which extended the indices to older ages and obtained separate estimates of *M* for different age groups, and
iii. A "rv" model, which was like the revised model except that it was calibrated with the RV indices only.

Comparisons between these models led to the following conclusions (Appendix III in Swain et al. 2009b):

1) Model results were very similar using the RV index alone versus also including the shorter time series of sentinel and commercial catch rate indices.
2) A number of discrepancies were evident between the survey indices and abundance predicted by the model with age-aggregated *M*. Using a model which estimated separate values of *M* for different age groups of cod removed these discrepancies. Nonetheless, it

was decided at that time (Swain et al. 2009b) to retain the standard model as the basis for advice on stock status, pending further work on estimating age-disaggregated patterns in *M*.

This section describes further work on estimating age-disaggregated time trends in *M* using population models. This work provides further support for the conclusion that the time trends in *M* differ between young and older southern Gulf cod.

3.2 METHODS

Ten population models are compared (Table 1). All are SPA models, either implemented using the ADAPT software (Gavaris 1988) or using AD Model Builder (ADMB) (http://admb-project.org/).

All of the ADAPT models estimate *M* in blocks of years starting from a period when *M* is fixed. The models differ in the following ways:

i. the years grouped together into "*M* blocks",
ii. the initial fixed values for *M*,
iii. the indices used for calibration, and
iv. whether *M* was estimated for all ages aggregated (2+) or separately for ages 2-4 and 5+.

In models with age-aggregated *M*, *M* in the initial block of years was fixed at 0.2, as has been the custom in previous assessments. In models with separate *M*'s for ages 2-4 and 5+, the initial fixed value for the 5+ group was set at 0.1, based on the studies (cited above) which indicated that *M* in the 1970s and earlier appeared to be lower than 0.2. For ages 2-4, initial *M* was fixed at either 0.4 or 0.5, based on the expectation that *M* should normally be higher for smaller fish (e.g., Gislason et al. 2010). These values are comparable with the values used for small cod in some east Atlantic assessments, as reported in an independent expert review of the southern Gulf of St. Lawrence cod assessment (DFO 2009). Model 1 is the same as model 1 in the last assessment (Swain et al. 2009b), except that the indices and catch-at-age have been updated with the 2009 data (and *M* is estimated for 1994-1998 instead of being fixed at 0.4). A detailed description of this model is given in Swain et al. (2009b, p.27-30). The other ADAPT models are the same as this model except as described in Table 1. Catch at age was for ages 2-15 yr for all ADAPT models except model 8, which had a plus group (12+). For the RV and sentinel trawl surveys, indices were at the scale of trawlable abundance.

The ADMB models were like the ADAPT models except that *M* was modeled as a random walk:

$M_{ij} = M\text{init}_j$ if $i = 1971$
$M_{ij} = M_{i-1j} * \exp(M\text{dev}_i)$ if $i > 1971$
$M\text{dev}_i \sim N(0, 0.1^2)$

where *j* indexes age group (2-4 or 5+) and *i* indexes year. *M*init was a parameter with starting (prior) values set at 0.4 and 0.2 for age groups 2-4 and 5+, respectively. Model 9 was the ADMB equivalent of ADAPT model 6, and model 10 was the ADMB equivalent of ADAPT model 8 (Table 1).

Chouinard et al. (2005) demonstrated that SPA can reliably estimate changes in age-aggregated *M*. Simulation testing was conducted to determine whether these models can reliably estimate age-dependent time trends in *M* (Appendix I). These tests used the ADMB models. These tests indicated that these models do not indicate changes in *M* when none occur and reliably identify the timing of changes. For ages 5+, the value of *M* was correctly estimated when F was low, but tended to be over-estimated when *F* was high. For ages 2-4, the ADMB

models tended to over-estimate the level of M, and had difficulty identifying a change in *M* when the change was in the same direction as the change in *F*.

3.3 RESULTS

3.3.1 Model fit

Residual patterns are shown for representative models in Figure 3. Patterns are most severe for Model 1, the standard assessment model. Patterns are less severe for models that estimate *M* separately for ages 2-4 and 5+ (all the other models in the figure). There is little pattern in the residuals for the models with a plus group (12+, models 8 and 10). Based on residual patterns, models 8 and 10 are the best models of those examined.

Figure 4 compares catchability-corrected RV abundance trends with model estimates for groups of ages and representative models. Models with age-aggregated *M* (models 1 and 2 in the figure) underestimate RV abundance of ages 2-4 in the 1970s and 1980s and overestimate abundance of these ages in the 1990s and 2000s. Models which estimate *M* separately for ages 2-4 and 5+ do not exhibit this problem (all the other models in this figure).

The sum of squared residuals (SSR) for a consistent block of RV indices is compared among models in Table 2. SSR is considerably greater for all models with an age-aggregated *M* (models 1, 2 and 5) than for models with separate 2-4 and 5+ *M* (the remaining models). SSR is lowest for the models with a plus group (Models 8 and 10). SSR is slightly lower for ADMB models than for their ADAPT equivalents (6 and 9, 8 and 10), but the ADMB models have many more parameters (a random walk deviate for each year). Based on SSR, the best models are the plus group models with separate *M* for ages 2-4 and 5+, and the worst models are the models with age-aggregated *M*.

Figure 5 compares estimated recruitment rates (the number of age-3 recruits produced per unit of spawning stock biomass) among models and with model-independent estimates based directly on the RV data. Models with age-aggregated (2+) *M* estimate that recruitment rates were very high in the 1990s and 2000s, much higher than the rates at the start of the time series and approaching the exceedingly high rates of the mid to late 1970s (Fig. 5a-c). In contrast, the RV data indicate that recruitment rates in the 1990s and 2000s were much lower than those in the mid to late 1970s and were comparable to those observed in the early 1970s (1971 and 1972 year-classes; Fig. 5d). The recruitment rates estimated by the models with separate 2-4 and 5+ *M* (Fig. 5e-k) are all consistent with the pattern indicated by the RV data. Like the results presented in Figure 4, these results indicate that models that estimate separate time trends in *M* for ages 2-4 and 5+ are more consistent with the data than those which estimate a single age-aggregated trend in *M*.

Estimated catchability coefficients for the RV survey are shown in Appendix 2 for the 10 models.

Conclusion: The data no longer support models which assume or fit a single age-aggregated time trend in *M*.

3.3.2 Natural mortality

Estimates of age-aggregated (2+) *M* resemble previously reported trends, with *M* increasing in the 1980s and remaining at high values throughout the 1990s and 2000s (Fig. 6). Estimates for the 2004-2009 period range between 0.64 and 0.71. The apparent timing of the increase depends on the blocks of years used to estimate *M*. Models 1 and 5 suggest a fairly steady increase throughout the 1980s and early 1990s. Model 2 suggests a sharp increase in *M* in the late 1980s and early 1990s.

Estimates of *M* for ages 2-4 and 5+ are shown in Figure 7 for ADAPT and ADMB models that do not use a plus group and in Figure 8 for the corresponding models with a plus group. Trends are very similar for all four models, though the level estimated for ages 2-4 differs between the ADAPT and ADMB models. The ADMB models estimate *M* to be very high (>1.2 in the 1970s and 1980s) for 2-4 year-old cod. These estimates seem high compared to estimates for similarly sized cod elsewhere (e.g. estimates of about 0.8 for age-1 cod in the North Sea). Likewise, using the growth parameters of southern Gulf cod in the 1970s, the formula recommended by Gislason et al. (2010) for estimating *M* from length and growth characteristics, and the average abundances at age in the 1970s from model 8, an estimate of the weighted average *M* for ages 2-4 would be 0.76 (the unweighted average would be 0.64). Simulation testing indicated a tendency for the ADMB model to overestimate age 2-4 *M* (Appendix I). Note that the increase in estimated 2-4 *M* in the early 1970s is an artifact of a constraint on the maximum value of *M*init. Although the level differs between ADAPT and ADMB models, all models show the same trend, with *M* of 2-4 year-old cod declining in the early 1990s.

Despite the difference between ADAPT and ADMB models in the estimated level of *M* for ages 2-4 yr, estimates of *M* for ages 5+ yr were very similar between the two types of models. The ADMB models estimated 5+ *M* to be near 0.1 in the early 1970s, consistent with the results of independent studies (discussed above). All four models estimated a slight increase in 5+ M in the late 1970s and early 1980s, followed by a rapid increase as the stock declined in the late 1980s and early 1990s. For all models, estimates for the 1990s and 2000s fluctuate around a high level. The increase in the late 1980s and early 1990s is considerably sharper in models 6 and 9 (no plus group) than in models 8 and 10 (12+ plus group). The average 5+ *M* estimate for 1990-2009 was 0.72 and 0.67 for models 6 and 9, respectively, and 0.65 and 0.58 for models 8 and 10, respectively.

Conclusion: Trends in *M* differ between cod aged 2-4 yr and those aged 5+ yr. For cod aged 2-4 yr, *M* declined in the early 1990s. For cod aged 5+ yr, *M* was low (near 0.1) in the early 1970s, increased slightly in the late 1970s and early 1980s, then increased sharply in the late 1980s and early 1990s, and has remained at a high level since then.

3.3.3 Biomass and abundance trends

The models incorporating a 12+ group in the catch at age and separate 2-4 and 5+ *M*'s provide the best fit to the data. The ADAPT version of this model (model 8) produces more credible estimates for the level of *M* for cod aged 2-4 yr than the ADMB model. Thus, model 8 is used here as the basis for advice.

Estimated spawning stock biomass (SSB) declined sharply in the early 1990s, and then more slowly following the initial closure of the directed fishery in 1993 (Fig. 9). SSB has been below the limit reference point since 2002. Estimated abundance of cod aged 5 years and older has been generally declining since the mid 1980s, with the sharpest declines in the early 1990s.

3.4 DISCUSSION

Changes in natural mortality of southern Gulf cod appear to be in opposite directions for young and old cod. For cod aged 2-4 yr, estimated *M* declined in the early 1990s. The lower *M* of these young cod in the 1990s and 2000s than in the 1970s and 1980s may be related to the reduced abundance of large piscivorous cod in the 1990s and 2000s (Benoît and Swain 2008) and reduced discard mortality following the severe reduction in fishing effort in 1993.

In contrast, estimated *M* of older (5+) cod increased sharply in the late 1980s and early 1990s as cod abundance declined. This is consistent with the hypothesis that cod fell into a predator pit as their abundance declined (Fig. 10). Under this hypothesis, the current high level of *M* for these cod is partly a predation-driven Allee effect (Gascoigne and Lipcius 2004). Cod abundance also declined to a low level in the mid 1970s but 5+ *M* was not unusually high then. This could reflect a much shallower predator pit then than now. Grey seals may be an important predator of southern Gulf cod (Benoît et al. 2011), and grey seal abundance was at a much lower level in the 1970s than in recent years (Hammill and Stenson 2011), providing a possible explanation for the hypothesized change in the depth of the predator pit.

It might be argued that a close positive correlation should be observed between cod *M* and grey seal abundance if grey seal predation is an important cause of high *M*. *M* was at a high level throughout the 1990s and 2000s, and did not increase with increasing seal abundance during this period. A number of factors may contribute to this apparent inconsistency. First, grey seal predation may have accounted for a lower proportion of *M* in the 1990s than in the 2000s. For example, it is likely that unreported catch accounted for a substantial portion of estimated *M* in the early to mid 1990s, but was a negligible component of *M* in more recent years (Swain et al. 2011). Secondly, a simple linear relationship between prey mortality and predator abundance may not occur for a number of reasons, such as prey switching when abundance of the focal prey declines to very low levels or abundance of alternate prey increases.

Another hypothesis for elevated *M* of cod in the Northwest Atlantic is that it might be partly due to life-history change (Hutchings 2005). Survival costs to reproduction are expected to increase as age and size at maturity decline. Hutchings (2005) suggested that elevated *M* might be partly due to fisheries-induced declines in age and size at maturity. Age and size at maturation of southern Gulf cod declined sharply in cohorts produced in the 1960s, likely reflecting an evolutionary response to intensified fishing, but have changed little since then (Swain 2011). In contrast to the expectation under this hypothesis, adult *M* was low in the 1970s. Costs to reproduction may be more evident under stressful physiological or ecological conditions (e.g., Reznick 1985). Condition of southern Gulf cod declined from the mid-1970s to the mid-1980s (Swain et al. 2009b), likely reflecting strong density-dependent effects within and among the exceptionally strong cohorts produced in the mid to late 1970s. Thus, the moderate increase in estimated *M* of adult cod in the late 1970s and early 1980s (Figs. 7 and 8) might reflect stressful ecological conditions interacting with a small size at maturity. If so, a decline in M due to this cause would be expected to have occurred as condition of cod improved in the late 1980s (Swain et al. 2009b).

The opposing changes in natural mortality between younger (smaller) and older (larger) fish, reported here for cod, are seen throughout the marine fish community of the southern Gulf. Based on changes in their abundance, mortality of small-bodied species appears to have declined to low levels in the 1990s and 2000s (Benoît and Swain 2008). Likewise, in large-

bodied species in addition to cod, mortality has declined for smaller individuals and increased for larger individuals in recent decades (Swain et al. 2009a; Benoît and Swain 2011).

4. MINIMUM DECREASE IN NATURAL MORTALITY REQUIRED TO RESTORE SOUTHERN GULF COD TO THE LIMIT REFERENCE POINT

4.1 INTRODUCTION

This section describes stochastic projections of future SSB of southern Gulf cod at the current level of natural mortality and at lower levels of *M* for 5+ cod. These projections assume that other components of productivity (recruitment rate, growth, *M* for 2-4 year old cod), as well as age at maturity, remain at the levels observed over the past 20 years. The goal is to determine the minimum decrease in 5+ *M* required to have a high probability of restoring this population to its limit reference point (LRP) of 80,000 t of SSB.

4.2 METHODS

Methods are the same as those used by Swain and Chouinard (2008). Projections were based on Model 8. For each level of *M*, the projection was iterated 1,000 times. For each iteration, one of the 1,000 bootstrap replicates of terminal abundance (abundance at age at the start of 2010) was randomly selected. The population was projected forward from this starting point. For each year of the iteration, 2-4 and 5+ *M*s were randomly selected from normal distributions with means and standard deviations (SD) equal to the estimates for these parameters and their SDs for the 2003-2009 period. Likewise, recruitment rates and weights-at-age were randomly selected from the values observed over the past 20 years. Fishery removals were assumed to be zero in all projections. See Swain and Chouinard (2008) for further details.

Recruitment in these projections is obtained by multiplying SSB by a recruitment rate randomly selected from those observed over the past 20 years. This assumes that there are no compensatory recruitment responses (increased recruitment rate at low SSB). This is supported by the stock and recruit data from the last 20 years (Fig. 11). Over this time period, the stock-recruit relationship does not differ from a straight-line relationship (with an intercept that does not differ significantly from 0). At some level of SSB greater than those observed over this period, one would expect a compensatory decline in recruitment rate. At projected levels of SSB greater than the maximum observed over this period (about 300,000 t), the SSB used to obtain recruitment was set at this maximum level.

4.3 RESULTS AND DISCUSSION

At the current levels of *M* and other components of productivity, SSB is projected to decline exponentially, reaching levels near extirpation (SSB < 1,000 t) in about 40-50 years (Fig. 12a). This result is similar to that reported by Swain and Chouinard (2008). If 5+ *M* declined from its current estimate of 0.629 to 0.5, the stock is still projected to steadily decline, with no chance of reaching the LRP (Fig. 12b). At a 5+ M of 0.45, the median projection is still a steady decline, but confidence bands about the median are very wide, and include a low probability (5%) of achieving the LRP within 20 yr (Fig. 12c). At values of 5+ M of 0.4 or lower, the stock is projected to increase rapidly, reaching the LRP in 20 years with probabilities of 70% at a 5+ M of 0.4 and 100% at a 5+ M of 0.35 (Fig. 12d and 13).

Note that these projections assume that there are no changes in *M* of 2-4 year old cod, which is fixed at the low level estimated for 2003-2009. If this level is low partly because of reduced predation by large cod, increases in *M* of small cod would be expected as the abundance of large cod increases.

5. ACKNOWLEDGEMENTS

ADMB programs used here are modifications of code provided by Bob Mohn; I thank Bob for this code and for discussion and advice during the course of this work.

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Table 1. Population models examined

Model	Name	Indices	*M*	intial *M*	M blocks
1	adapt 1M a	assessment	2+	0.2	(1971-1979), 1980-1986, 1987-1993, 1994-1998, 1999-2003, 2004-2009
2	adapt 1M b	assessment	2+	0.2	(1971-1976), 1977-1982, 1983-1989, 1990-1995, 1996-2002, 2003-2009
3	adapt 2M a	assessment	2-4, 5+	0.4, 0.1	(1971-1976), 1977-1982, 1983-1989, 1990-1995, 1996-2002, 2003-2009
4	adapt 2M b	assessment	2-4, 5+	0.5, 0.1	(1971-1976), 1977-1982, 1983-1989, 1990-1995, 1996-2002, 2003-2009
5	adapt 1M rv	rv 2-12	2+	0.2	(1971-1979), 1980-1986, 1987-1993, 1994-1998, 1999-2003, 2004-2009
6	adapt 2M rv a	rv 2-12	2-4, 5+	0.5, 0.1	(1971-1976), 1977-1982, 1983-1989, 1990-1995, 1996-2002, 2003-2009
7	adapt 2M rv b	rv 2-12	2-4, 5+	0.4, 0.1	(1971-1979), 1980-1986, 1987-1993, 1994-2001, 2002-2008
8	adapt 2M rv 12+	rv 2-10	2-4, 5+	0.5, 0.1	(1971-1976), 1977-1982, 1983-1989, 1990-1995, 1996-2002, 2003-2009
9	admb 2M rv	rv 2-12	2-4, 5+	-	random walk
10	admb 2M rv 12+	rv 2-10	2-4, 5+	-	random walk

Note: *M* was assigned a fixed value (the initial *M*) in blocks in parentheses, and estimated in other blocks. ADAPT models failed for some sets of *M* blocks, e.g., the blocks used for models 1 and 5 could not be used for the age-dependent *M* models. Assessment indices include the RV survey (1971-2002,2004-2009), the mobile sentinel survey (2003-2009), the sentinel longline index (1995-2009), a commercial CPUE index (1982-1993, trend in catchability), and several additional sentinel indices (1995-2002). Details are given in Swain et al. (2009). For Models 5-10, which are calibrated using the RV data only, RV data for 2003 are included in the calibration. (The 2003 data are sometimes excluded from analyses because they were collected by the CCGS *Wilfred Templeman*, which has not been calibrated to the other vessels used in the September survey; however, it is the sister ship of the CCGS *Alfred Needler*, which has been calibrated for this survey.)

Table 2. Sum of squared residuals (SSR) for the RV survey index for a block of years (1971-2002, 2004-2009) and ages (2-10) common to all models.

Model	Name	SSR
1	adapt 1M a	89.776
2	adapt 1M b	86.644
3	adapt 2M a	65.468
4	adapt 2M b	65.475
5	adapt 1M rv	88.849
6	adapt 2M rv a	65.661
7	adapt 2M rv b	72.750
8	adapt 2M rv 12+	51.212
9	admb 2M rv	61.602
10	admb 2M rv 12+	46.814

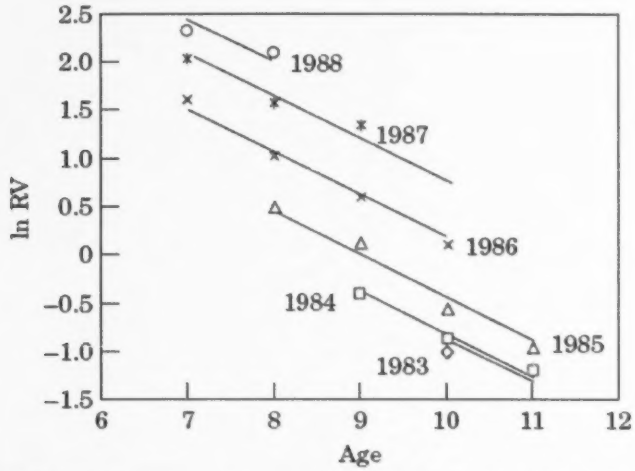


Figure 1. Fit of the analysis of covariance model to the data for the 1993-1996 period (from Sinclair 2001). Year-classes are labelled and plotted with different symbols. The model estimates a common slope (Z) with separate intercepts for each year-class.

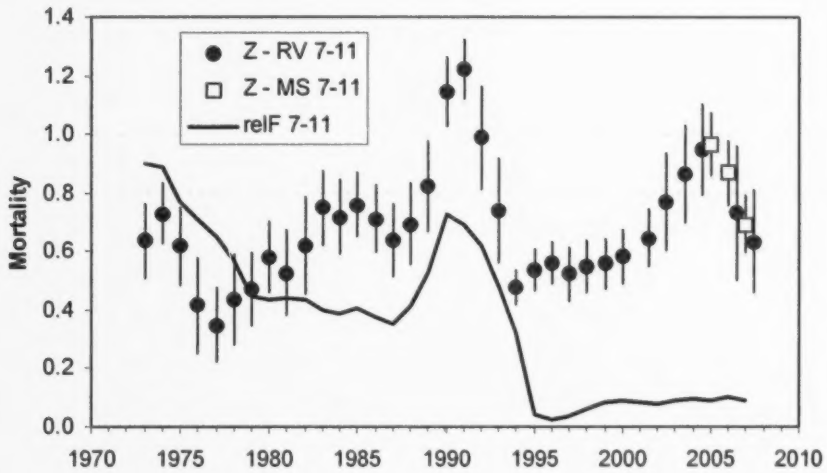


Figure 2. Estimated total mortality (Z) in moving 5-yr windows for cod aged 7-11 yr, based on catch rates in the September RV survey (filled circles) and mobile sentinel survey (open squares). Vertical lines are approximate 95% confidence intervals. The line is relative fishing mortality for ages 7-11, averaged over the same 5-yr periods.

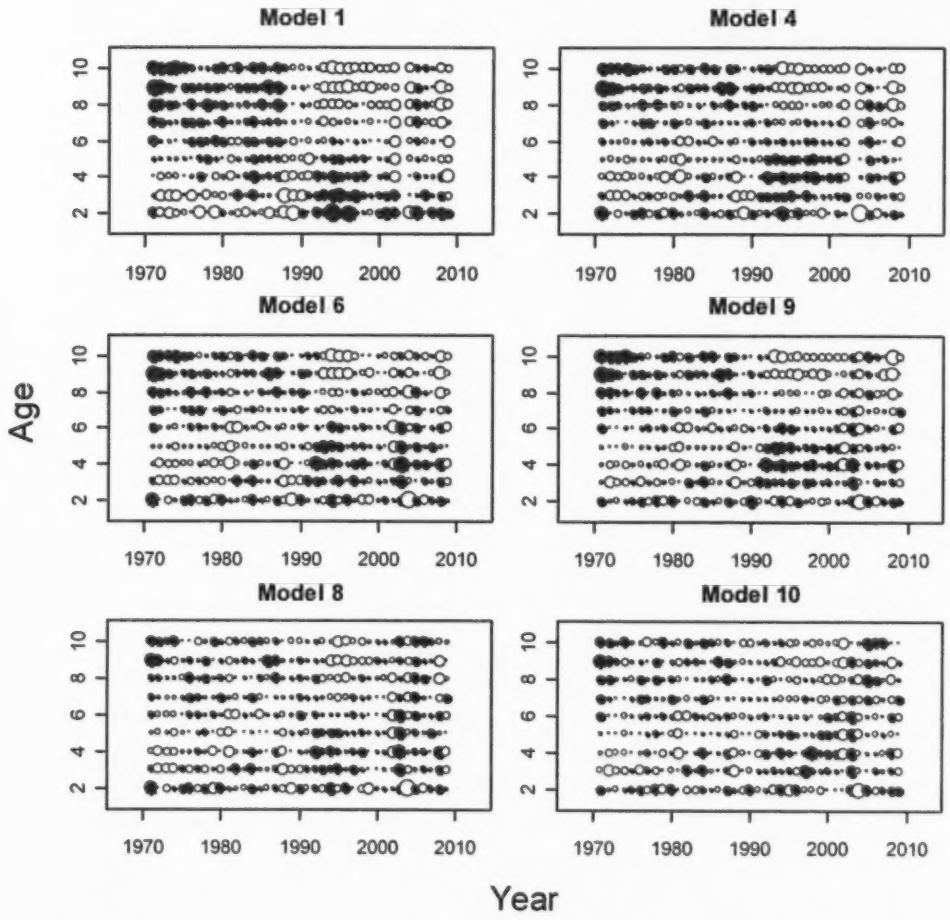


Figure 3. Residuals from the RV survey indices for selected models. Residuals are shown for a consistent block of ages (2-10 yr). Negative residuals are black (RV < SPA).

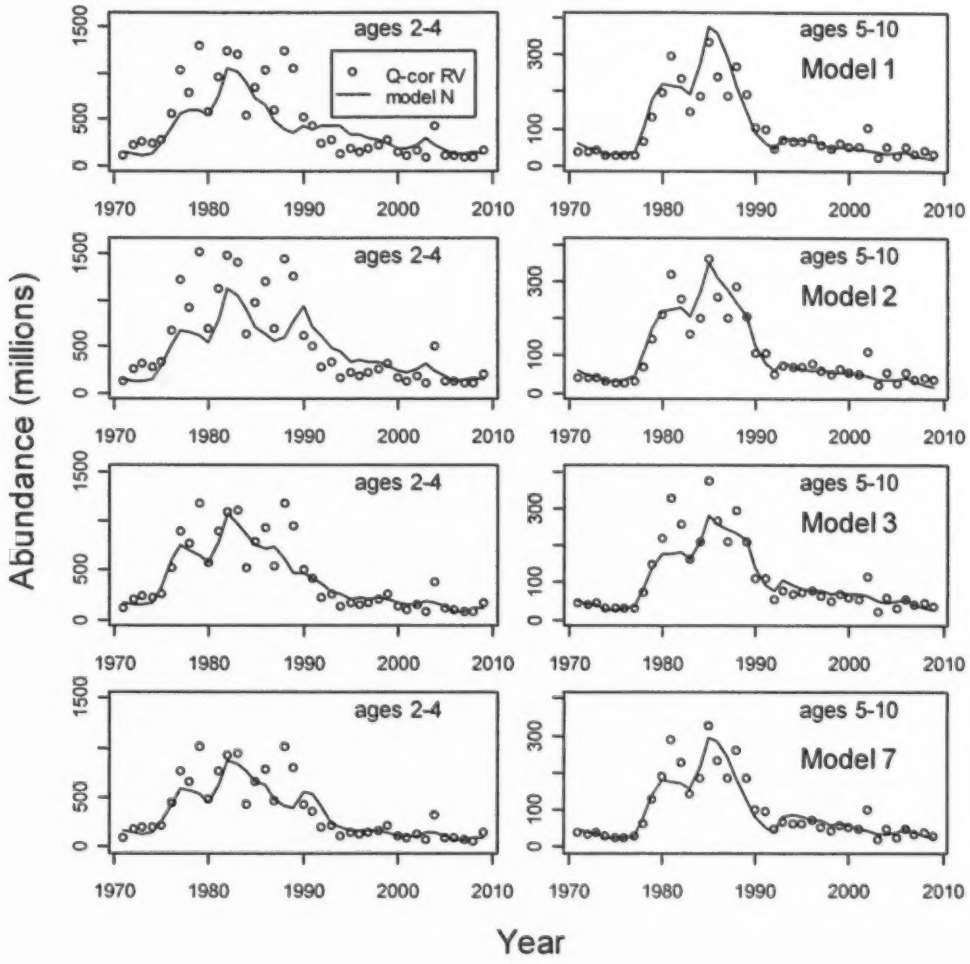


Figure 4a. Comparison of catchability-corrected RV survey abundance indices and abundance estimates from models. Models 1 and 2 estimate age-aggregated trends in M. Models 3 and 7 estimate separate trends in M for ages 2-4 and 5+.

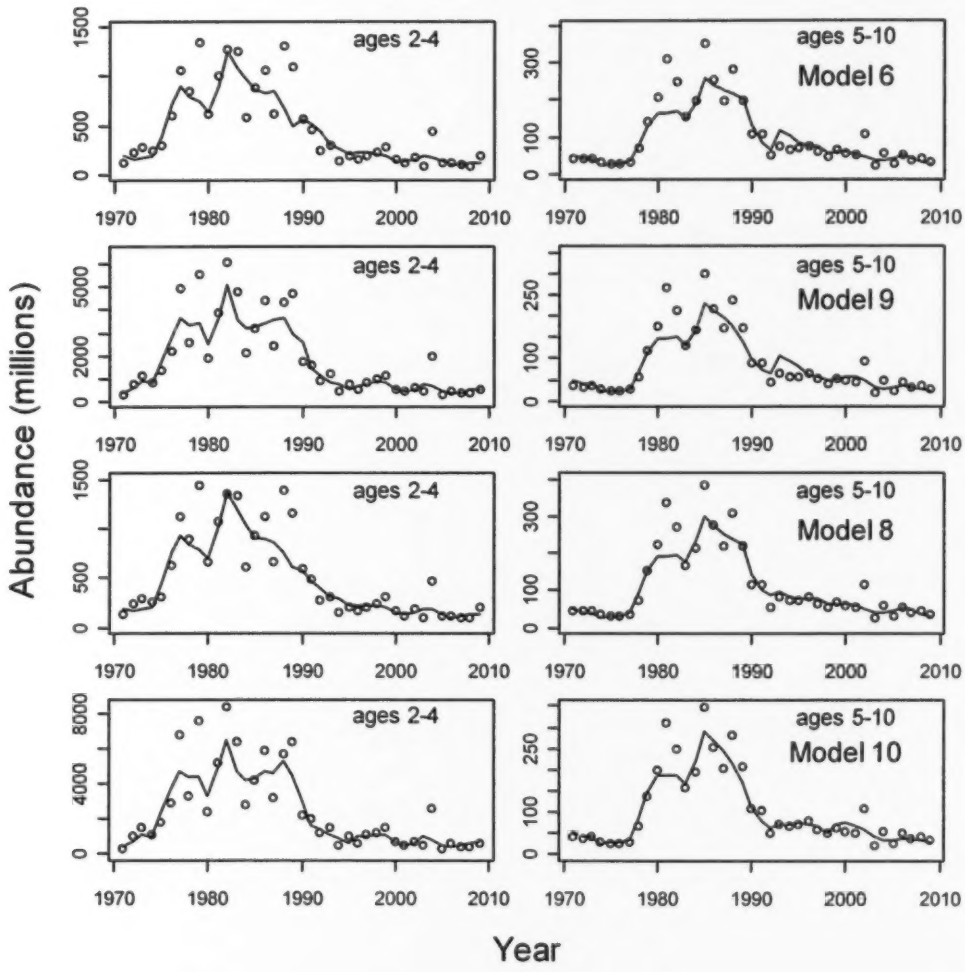


Figure 4b. Comparison of catchability-corrected RV survey abundance indices and abundance estimates from models. All these models estimate M separately for ages 2-4 and 5+. Models 8 and 10 have a 12+ group. Models 9 and 10 are the ADMB equivalents of ADAPT models 6 and 8. Note the change in scale between the ADMB and ADAPT models.

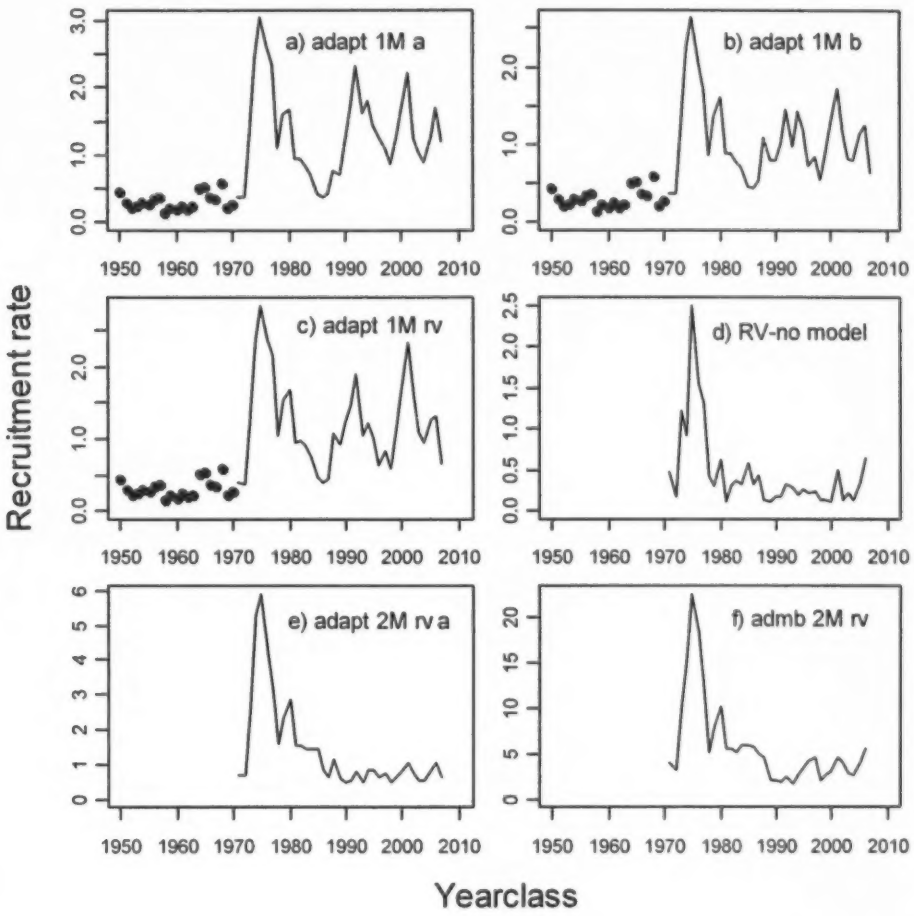


Figure 5. Recruitment rate (the number of age-3 recruits produced per unit of spawning stock biomass) estimated by the models or directly from the survey data (panel d). Panels are identified by model name: 1M- age-aggregated M, 2M – separate 2-4 and 5+ M; a,b – different M blocks; rv – calibrated with RV indices only; 12+ - a 12+ group is used (model numbers corresponding to the names are given in Table 1). Circles are the rates from an earlier SPA model which assumed an age-aggregated M of 0.2 (Maguire et al. 1983).

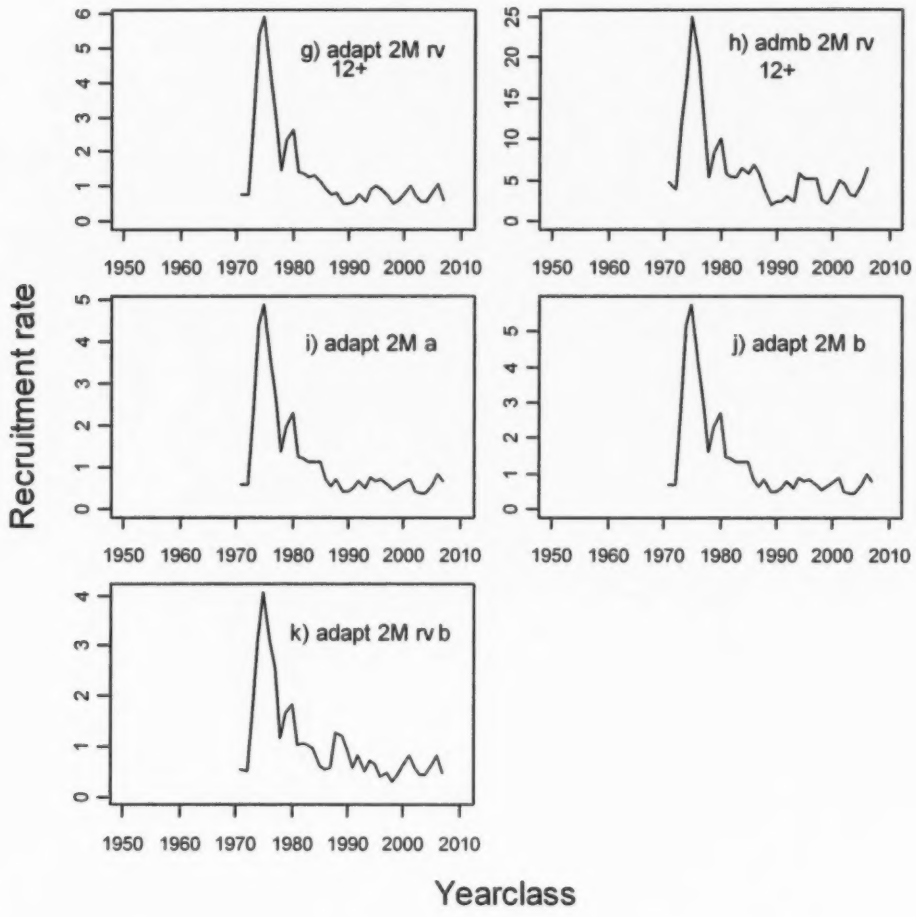

g) adapt 2M rv 12+
h) admb 2M rv 12+
i) adapt 2M a
j) adapt 2M b
k) adapt 2M rv b
Recruitment rate
Yearclass
1950 1960 1970 1980 1990 2000 2010

Figure 5 (continued).

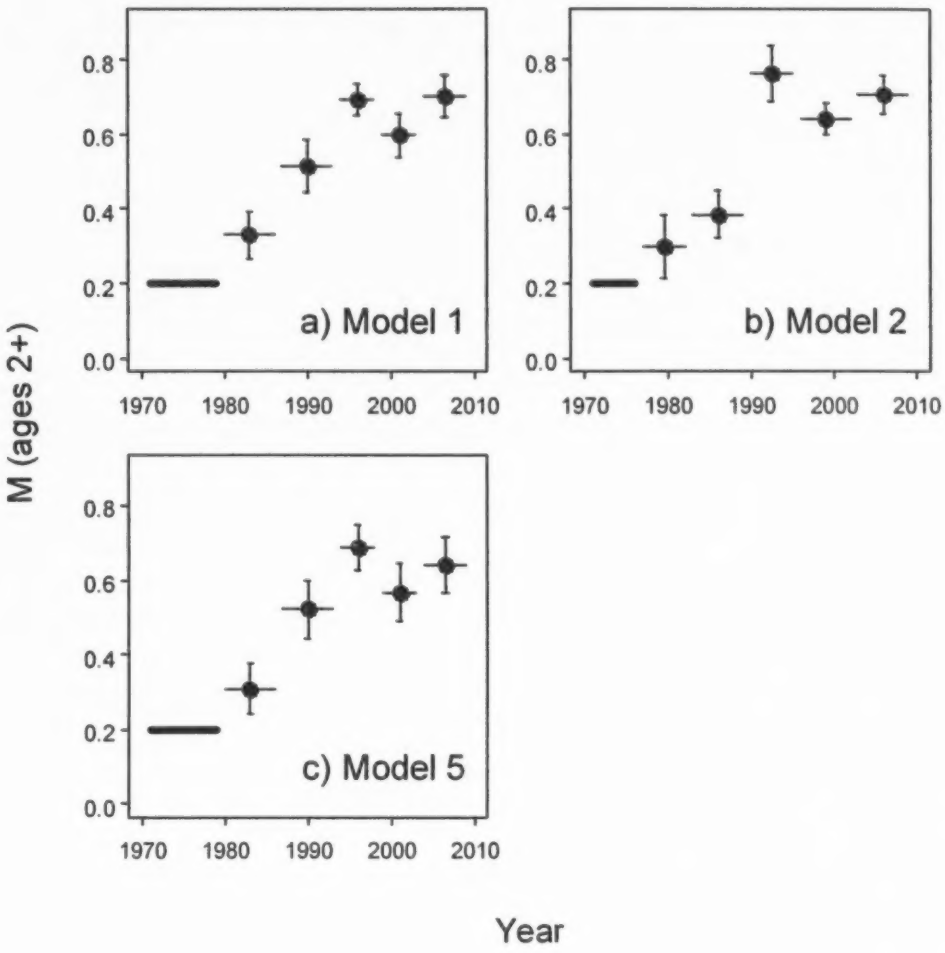


Figure 6. Estimates of age-aggregated (2+) M. Heavy horizontal line is an assumed value. Light horizontal lines indicate the time period for each estimate. Vertical lines are ± 2 SE.

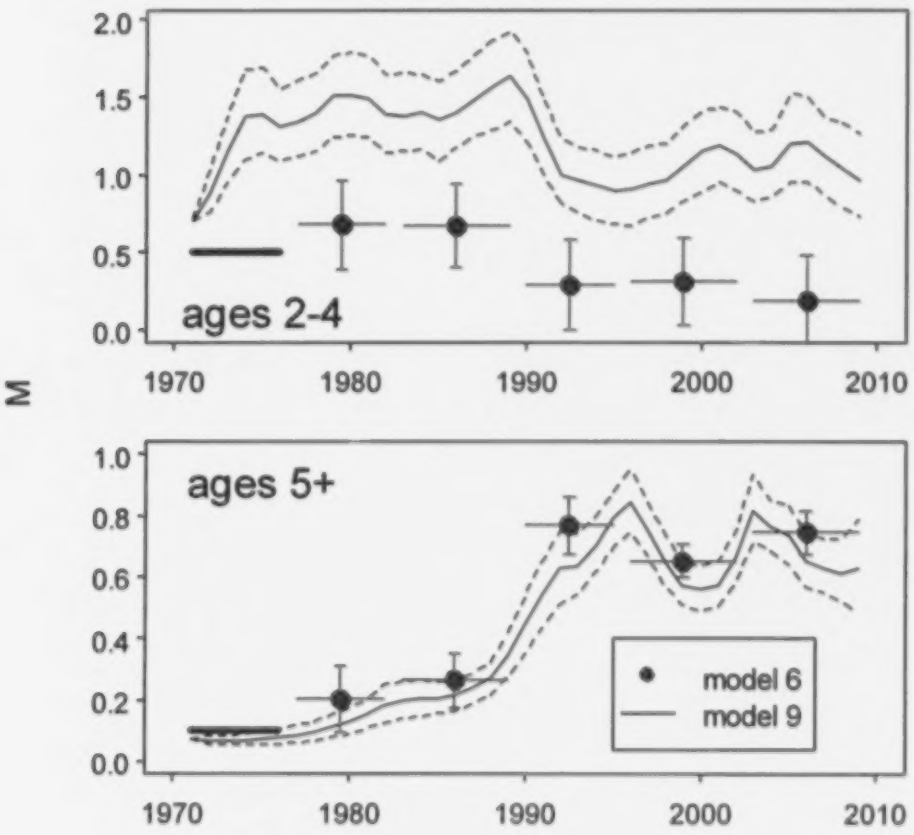


Figure 7. Age-dependent trends in M estimated by models 6 (ADAPT) and 9 (ADMB). These models use catch at ages 2-15 and are fit to RV indices for ages 2-12. The solid black line shows the median estimate and the dashed lines the 2.5th and 97.5th percentiles. Details for model 6 are as described in the Figure 6 caption.

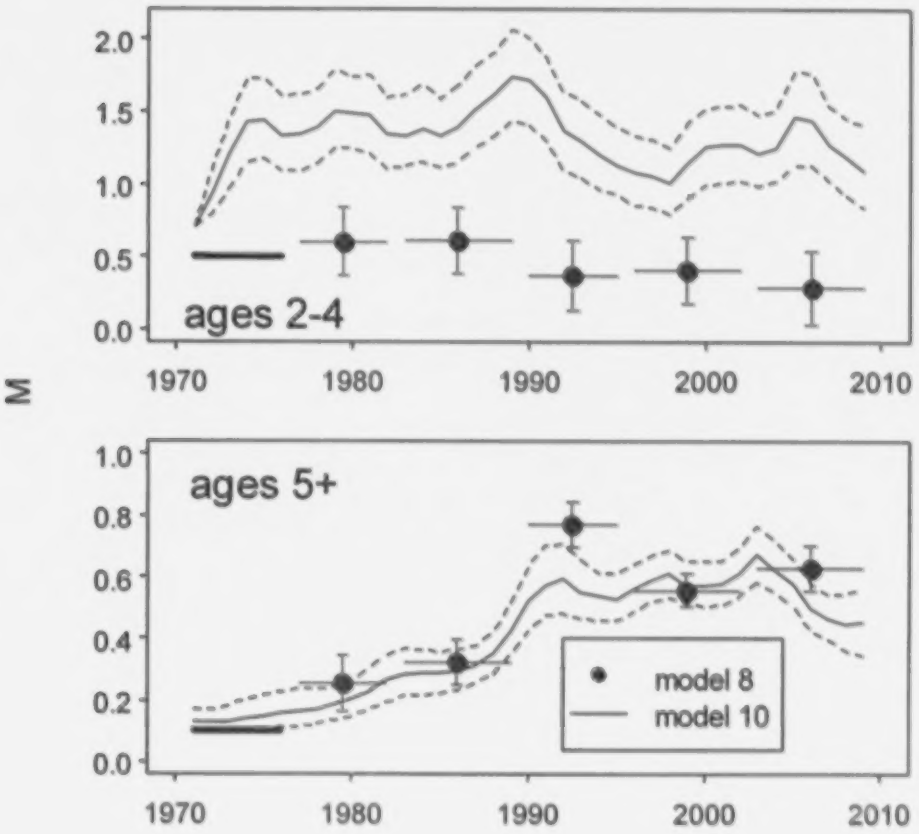


Figure 8. Age-dependent trends in M estimated by models 8 (ADAPT) and 10 (ADMB). These models use catch at ages 2-12+ and are fit to RV indices for ages 2-10. Further details are given in the Figure 7 caption.

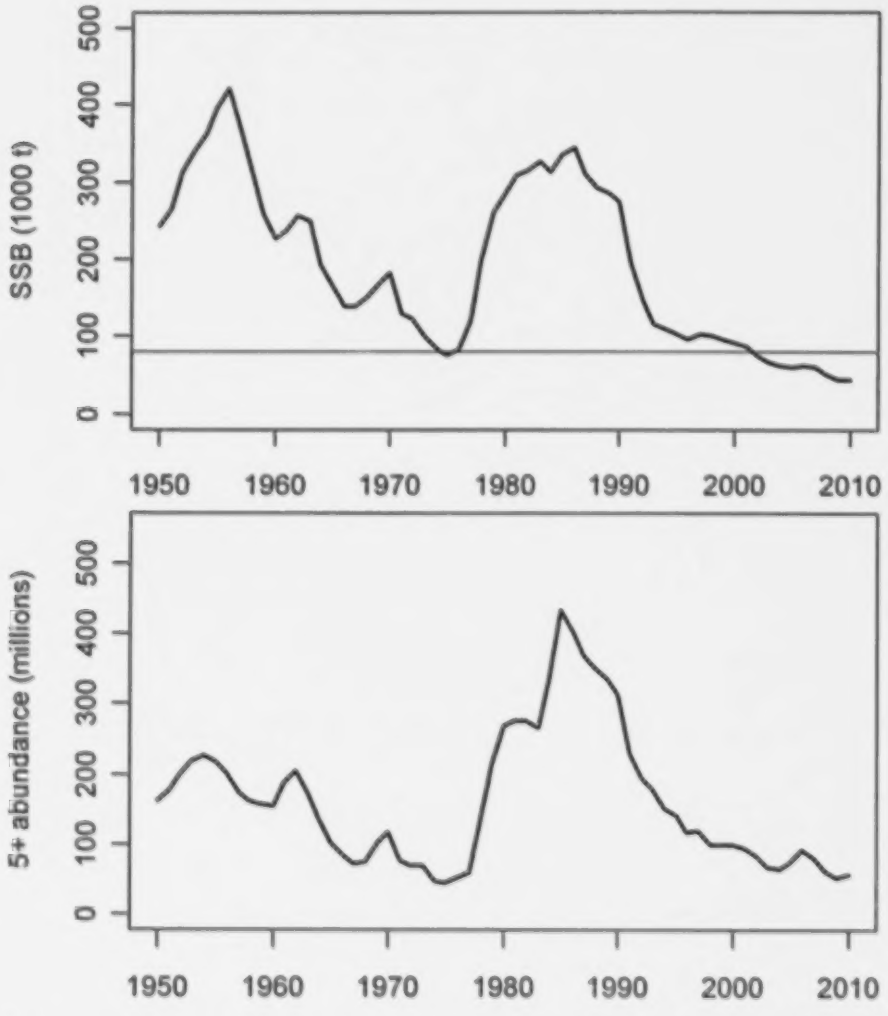


Figure 9. Estimated trends in spawning stock biomass (SSB) and 5+ abundance of southern Gulf of St. Lawrence cod. Trends for 1950-1970 are based on the model described in Maguire et al. (1983); trends for 1971-2010 are based on the preferred model (model 8) from the analyses in this study. The red horizontal line in the top panel is the limit reference point for this stock (80,000 t SSB).

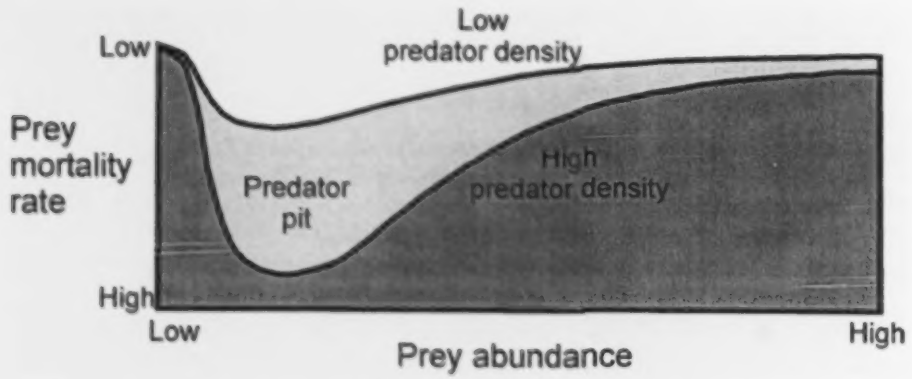


Figure 10. Schematic diagram of a predator pit. Redrawn from Bakun (2006).

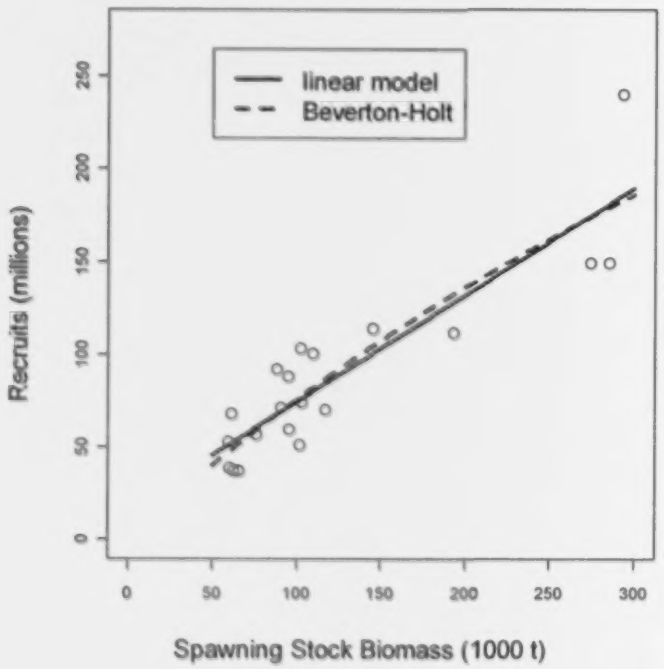


Figure 11. Stock – recruit relationship of southern Gulf cod for the 1988 to 2007 year-classes.

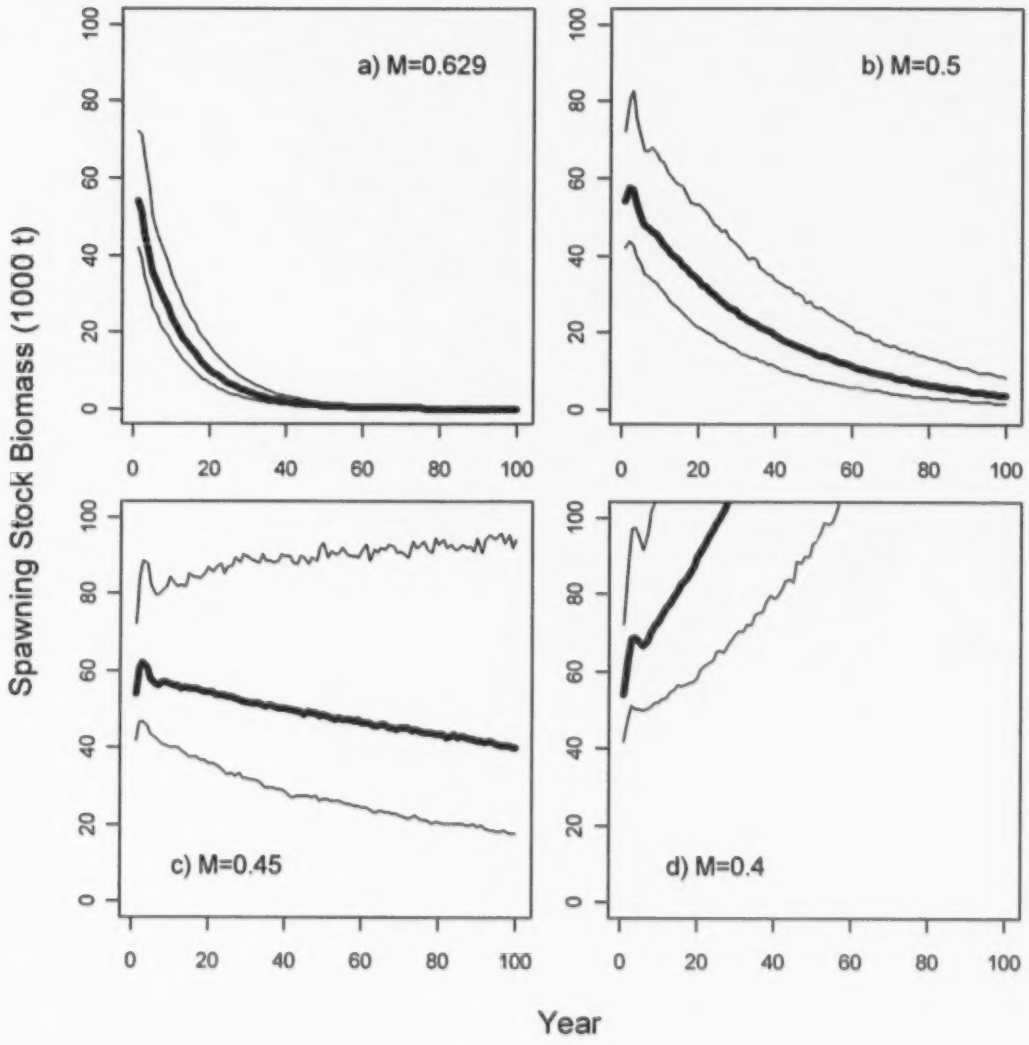


Figure 12. Projected SSB of southern Gulf cod at 4 levels of M for cod aged 5 years and older. Heavy line is the median projection and light lines are the 2.5th and 97.5th percentiles.

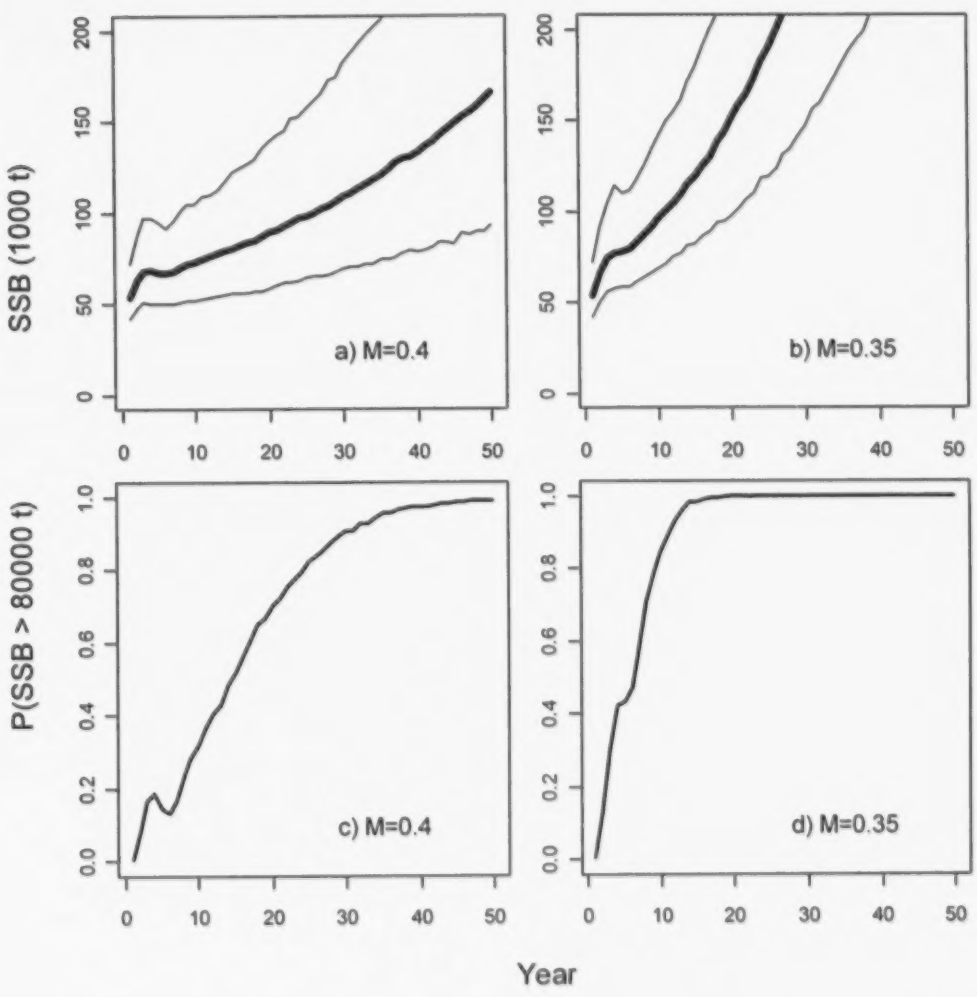


Figure 13. Projected SSB of southern Gulf cod and probability that SSB will exceed the limit reference point of 80,000 t, at two levels of M for cod aged 5 years and older. In panels a and b, heavy line is the median projection and light lines are the 2.5th and 97.5th percentiles.

Appendix I: Simulation testing of ADMB models estimating separate trends in *M* of cod aged 2-4 and 5+ years.

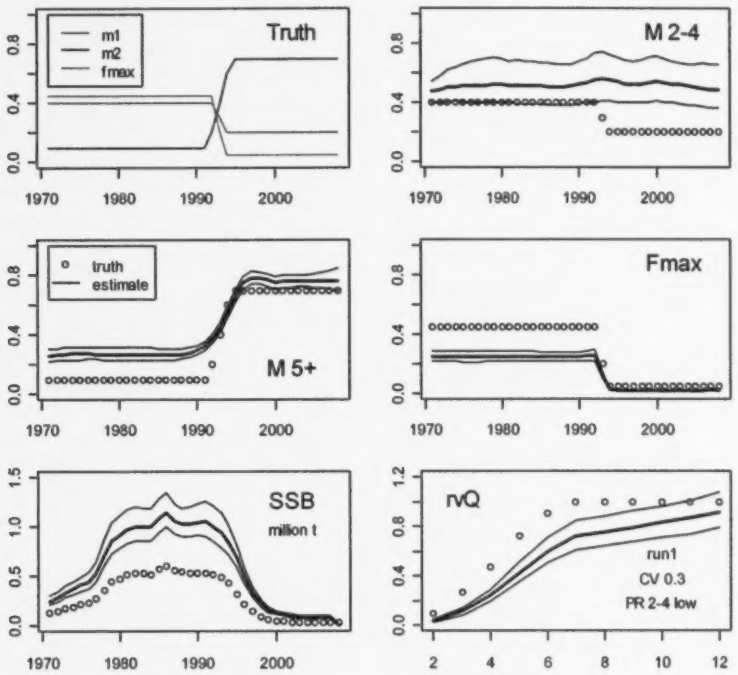
Methods

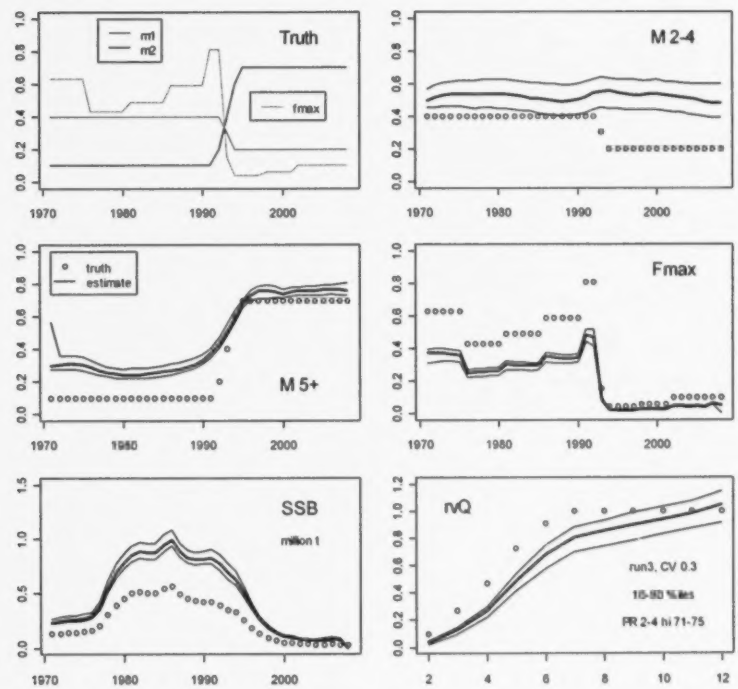
Synthetic populations (1971-2008 time series, ages 2-15) were generated as follows. Abundances at ages 2-15 in 1971 and at age 2 in all other years were set equal to estimated abundances from a model similar to model 3. This set variation (and autocorrelation) in year-class strength at levels similar to those observed in the southern Gulf population. The population was then projected forward using given patterns in *M* and *F*. Survey indices were generated by fishing the population with given age-dependent catchability. Survey indices were then perturbed by applying random lognormal error to produce indices with a CV of 20 or 30% (average CV of the observed indices for ages 2-10 is 20%). The resulting catch at age and survey indices were then used to estimate the *M* and *F* patterns. For each set of inputs (*M*, *F*, partial recruitment [PR] pattern to the fishery), this procedure was repeated 1,000 times.

Results

Results are summarized in the following figures. In each figure, the top left panel shows the true trends in m1 (*M* for ages 2-4 yr), m2 (5+ *M*), and fully-recuited *F*. The remaining panels compare the true values (circles) with their estimated values (lines). The heavy line is the median estimate and the light lines the 2.5^{th} and 97.5^{th} percentiles of the estimated values (unless otherwise specified).

(Note: In earlier runs, SSB was not calculated in the last year due to an omission in the simulation code. This results in an apparent sudden drop in estimated SSB in the last year in these runs.)


m1
m2
fmax
Truth
M 2-4
truth
estimate
M 5+
Fmax
SSB
million t
rvQ
run1
CV 0.3
PR 2-4 low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Truth
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Fmax
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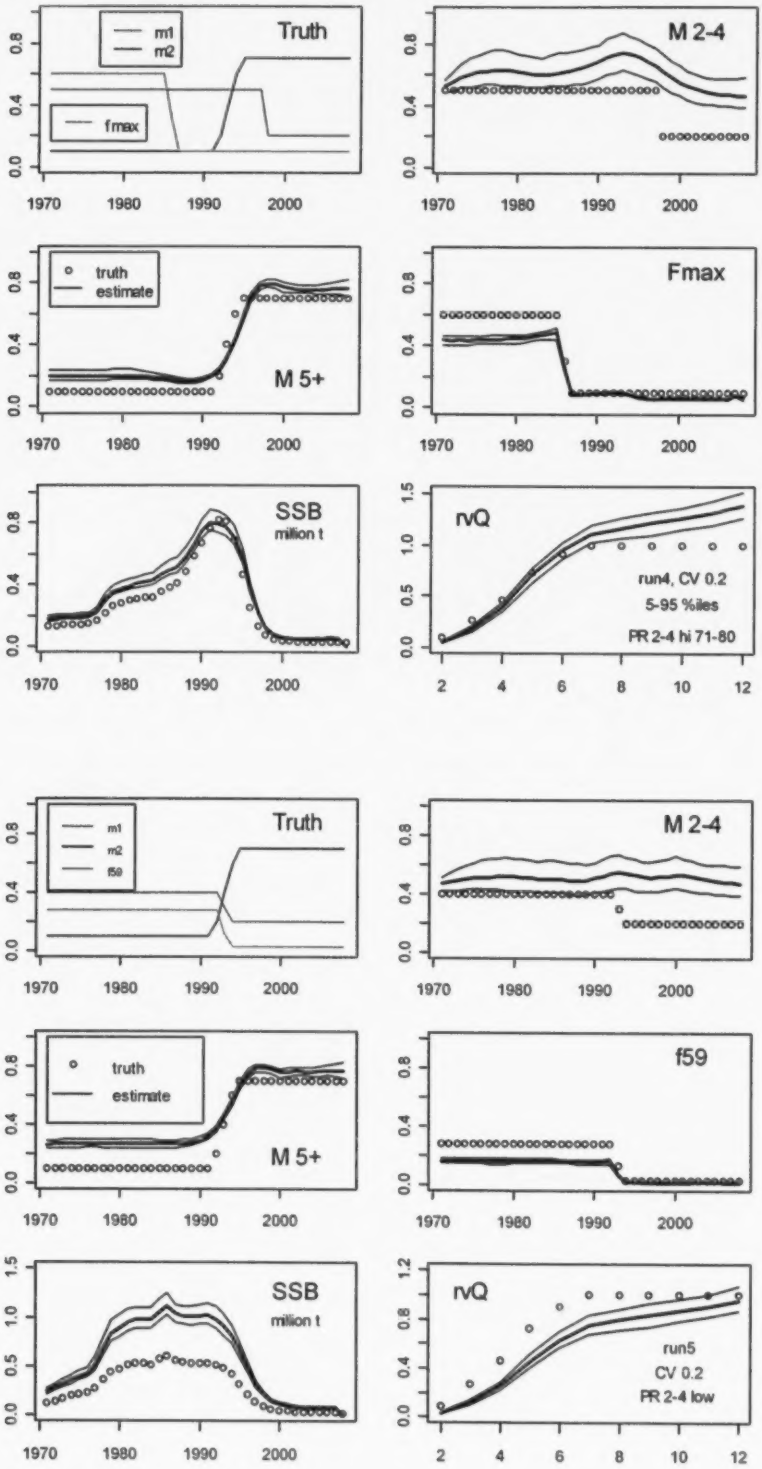
rvQ
run3, CV 0.3
PR 2-4 hi 71-75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m2
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M 2-4
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M 5+
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SSB
million t
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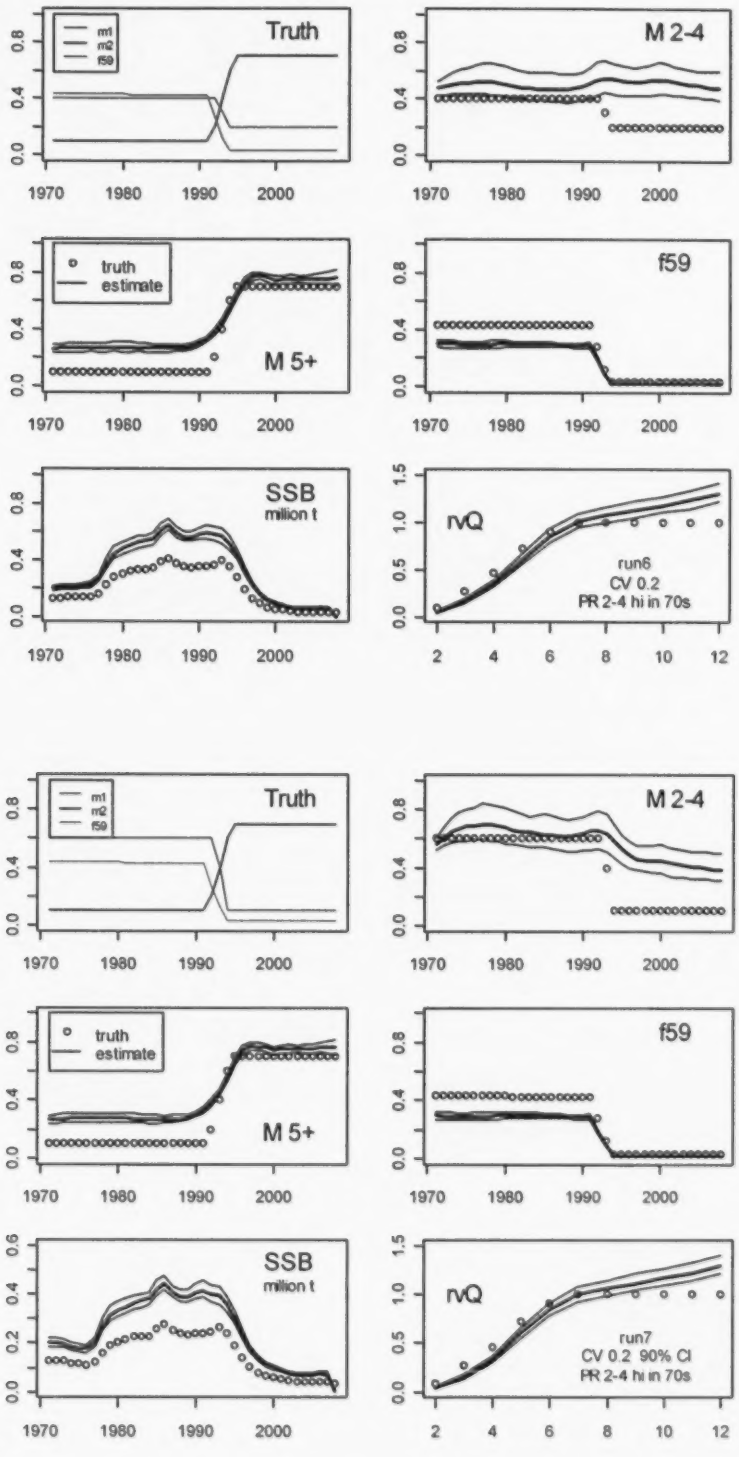
CV 0.2
PR 2-4 low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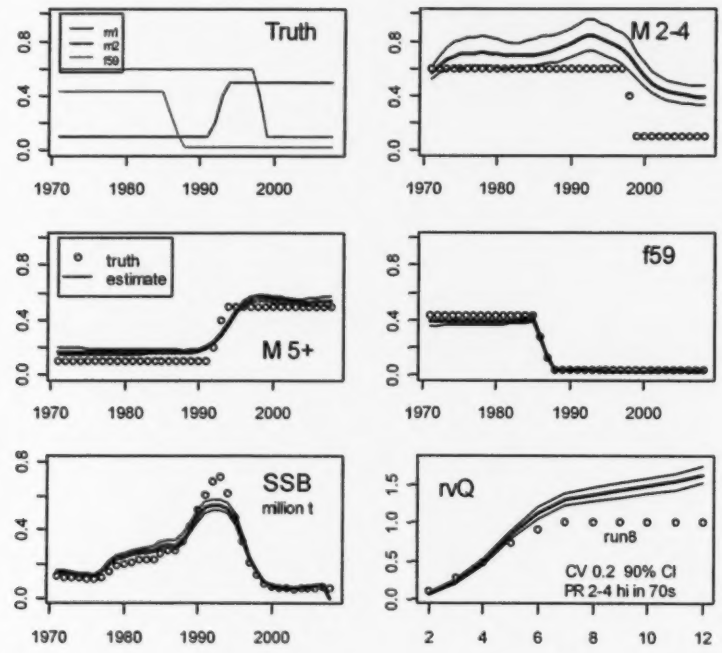
PR 2-4 hi in 70s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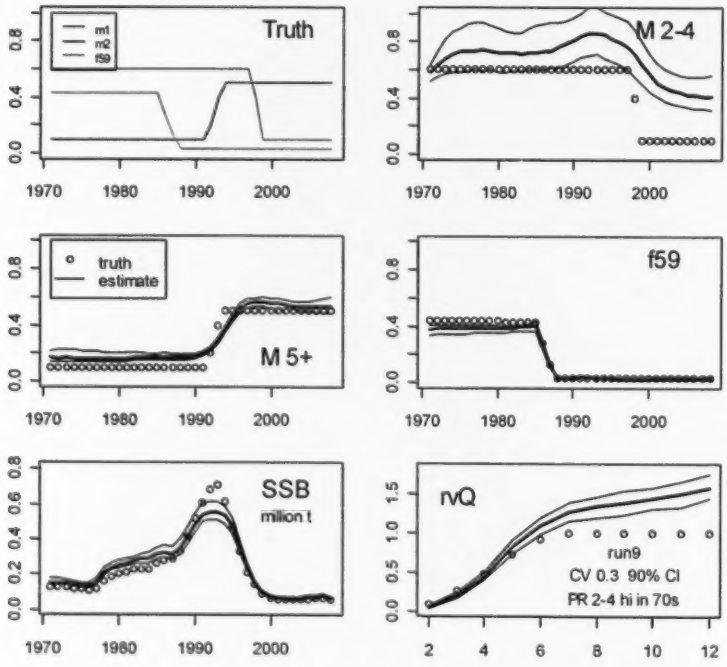
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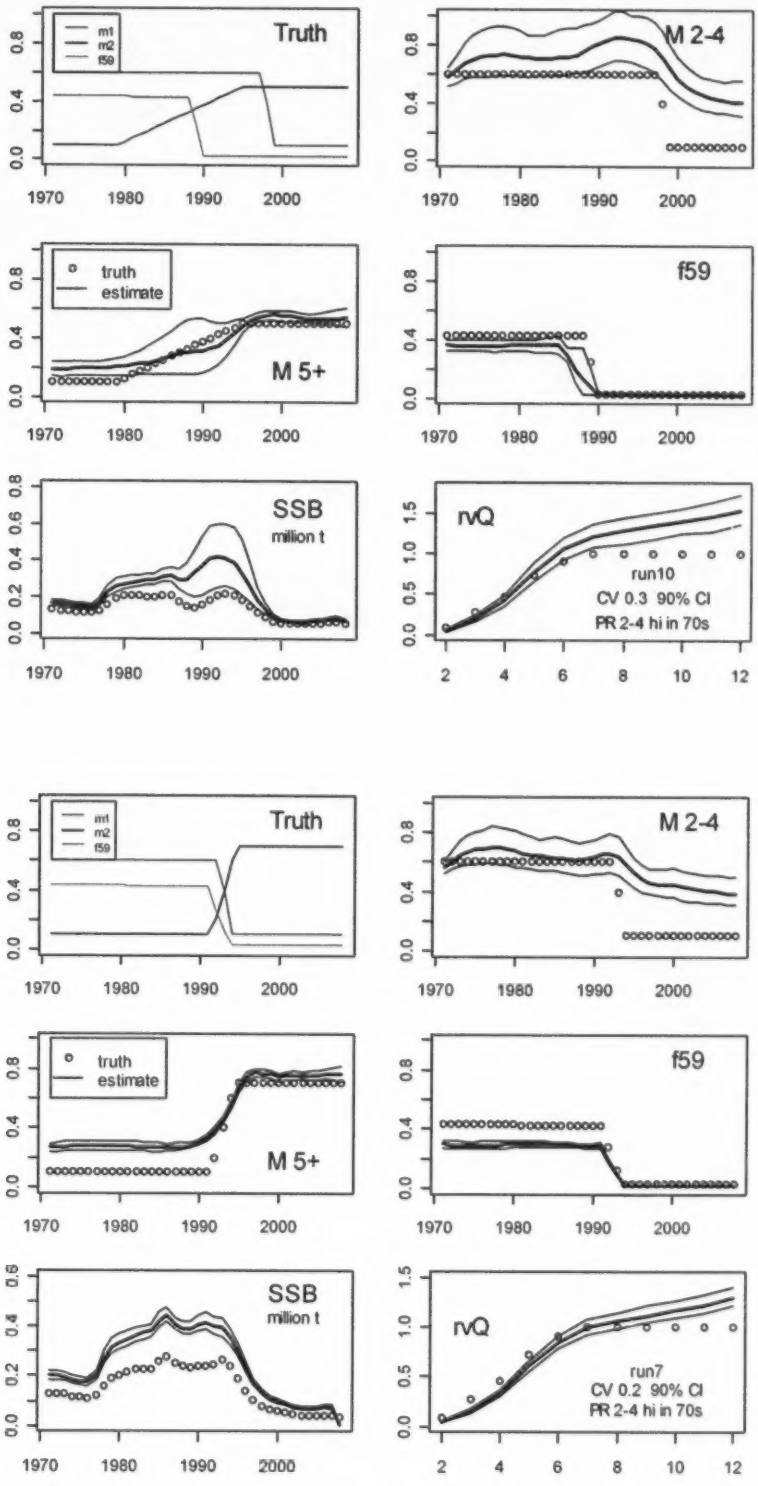
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PR 2-4 hi in 70s
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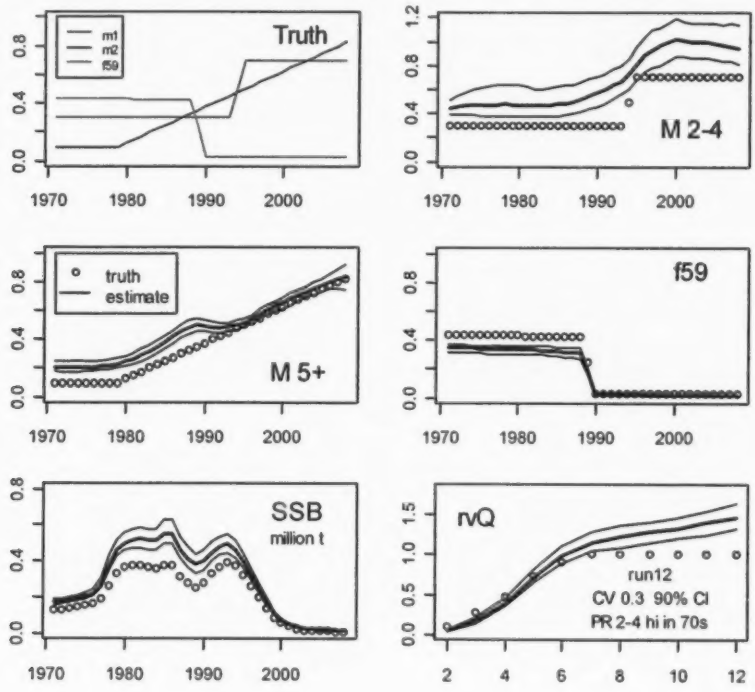
CV 0.2 90% CI
PR 2-4 hi in 70s


m1
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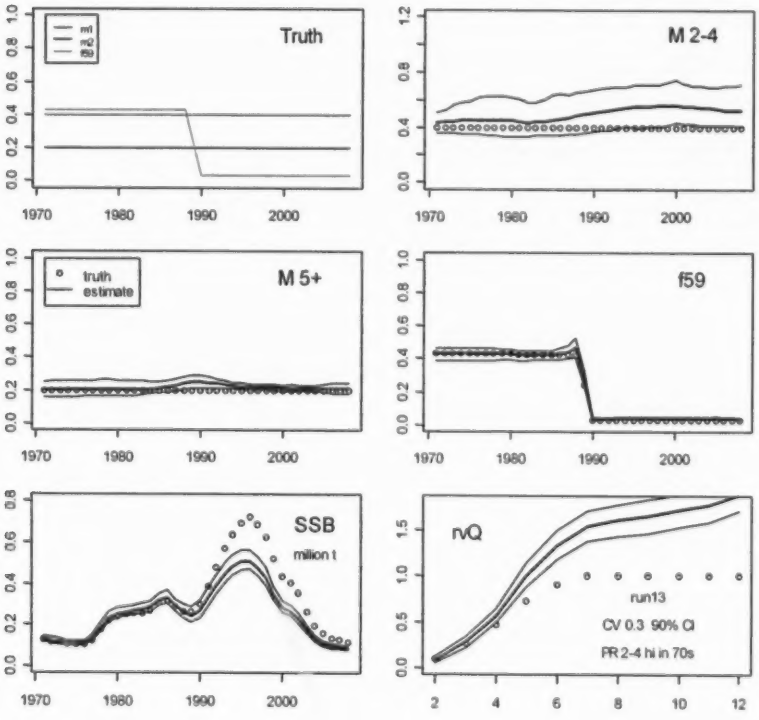
CV 0.3 90% CI
PR 2-4 hi in 70s


m1
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CV 0.3 90% CI
PR 2-4 hi in 70s

Appendix II: Estimated RV catchability coefficients.

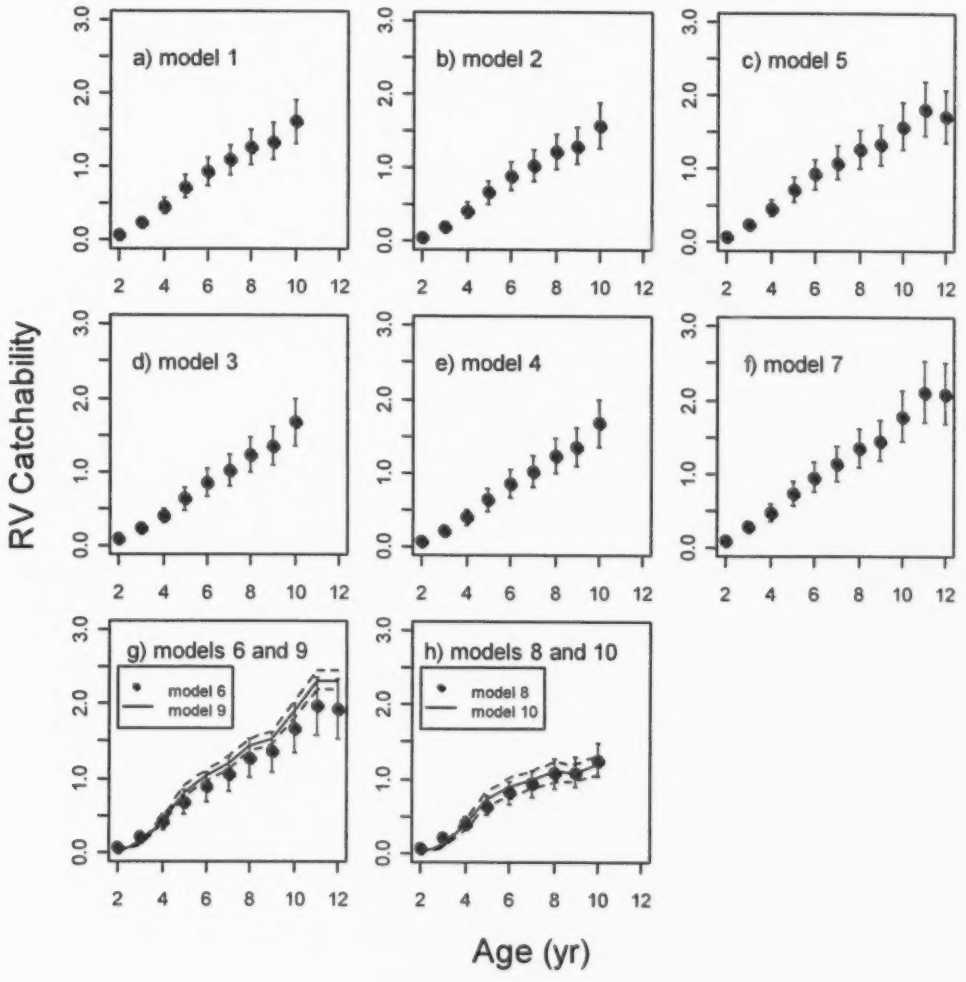

Figure A2. Model estimates of RV catchability coefficients. Circles are estimates from ADAPT models ± 2SE. Lines are estimates from ADMB models (median of 1,000 MCMC iterations and 2.5th and 97.5th percentiles).

Notes: RV indices are at the scale of trawlable abundance, with the area swept by a standard tow based on wing spread. This underestimates the true area fished due to herding of fish into the path of the trawl by the doors. For the RV survey, door spread is three or more times wing spread. Thus, catchability estimates greater than one are possible. However, catchability estimates much greater than one would imply very high fishing efficiency by the survey trawl.